SOME OBJECTIVES FOR EARTHWORM RESEARCH

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НЕКОТОРЫЕ ЗАДАЧИ ИССЛЕДОВАНИЯ ДОЖДЕВЫХ ЧЕРВЕЙ

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Introduction

The basic aim of soil zoology, and of the broader field of soil biology, is to understand biological processes in soils so that they might be better utilized and manipulated to enhance soil fertility and plant production. The general theme of this Colloquium, "Soil fauna and soil fertility", addresses this basic aim.

As soil zoologists we should give priority to investigations of the taxonomy, ecology, behaviour and physiology of those soil animals that are most widespread and numerous and that mostly affect the physical and chemical characteristics of soils. We should use the understanding we gain to manipulate populations to maximize their beneficial effects on soil fertility and plant growth.

The beneficial effects of earthworms on soils were first realized and described by Darwin /4/. A comprehensive treatment of this subject may be found in /8/. In this paper I intend to discuss two aspects of earthworm research that seem to me to provide especially important opportunities for research. They concern (a) the selection of species and genotypes within species that might be deliberately introduced into new environments to maximize the beneficial effects of earthworms on soil fertility and plant growth, and (b) some aspects of the role of earthworms in the decomposer cycle, especially in relation to the availability of nitrogen and phosphorus for plant growth.

Manipulation of Earthworm Populations

Modification by man of earthworm populations has been in the past and continues to be accidental or, where it is deliberate, to be based on fortuitous introductions in the past. Changes in land use to enable the development of productive pastures or crops have resulted in many parts of the world in the elimination of indigenous earthworms. These changes have been accompanied in many cases by the introduction of exotic earthworms that were included in soil with plants that have been introduced to geographical regions outside their natural range. Subsequent spread of the exotic earthworm species has also been fortuitous, except in a few cases, and the selection of species introduced and subsequently spread relates to the geographical origins of the introduced plants and not to the suitability of the earthworms as promoters of soil fertility in the new regions.

There are about 3000 species of earthworms. Of these, about 100 are peregrine, i.e. they have spread, with man, far beyond their original areas of distribution and have established themselves in man-modified environments. The origins of the peregrine species and their present distribution patterns relate to patterns of human migration. In temperate regions of the world they are mainly Lumbricidae from northern and western Europe, while in tropical regions they are mainly glossoscolecids, megascolecids and moniligastrids from South America, Africa and southern Asia. Some of the peregrines have been spectacularly successful in new environments and we should enquire into the reasons for their success and into how we might optimize their distribution to promote their beneficial effects on soil fertility and plant growth. We should also appreciate that there remains a large pool of species that have not been in a position to be spread by man. Among these there may be species that could be selected on the basis of a sound knowledge to their taxonomy, ecology, behaviour and physiology, and that might be well suited to particular environments far from their origins. Selection might be made first of suitable species, but we should also take into account the differences between genetic variants within species. There is much evidence of intraspecific genetic variability in earthworms that may relate to behavioural and physiological differences between genetic strains that are significant in their success as immigrants.

Selection of species. About 20-30 species of European Lumbricidae have been spread within the last few hundred years throughout temperate and some upland tropical regions of the world, and a few of these species are now the dominant earthworms of agricultural, pastoral and horticultural lands in these regions /8/.

Introduced lumbricids have probably attained maximum population levels and their most significant beneficial effects on soil fertility in New Zealand pastures. Species associations in New Zealand pastures rarely comprise more than three species, Aporrectodea caliginosa (and/or A.longa), Lumbricus rubellus and Octolasion cyaneum. There is commonly a succession of these species following clearing of native vegetation and its replacement by pasture. O.cyaneum frequently becomes established first, and in soils of low fertility the succession may go no further, with low abundance (up to c. $100/m^2$) and O.cyaneum the dominant species. In more fertile soils with more productive pastures earthworm populations change progressively, with increasing proportions of L.rubellus and A.caliginosa (and/or A.longa). In highly productive pastures abundance is commonly $500-1000/m^2$ and may exceed $2000/m^2$, with Apporectodea spp. and L.rubellus the dominant species. Introduction of lumbricids (A.caliginosa and L.rubellus) to pasture where they were formerly absent has led to increases of up to 70% in spring production of New Zealand grasslands /15/. Stockdill has estimated that there remain c. 2 million hectares of New Zealand pastures that do not at present have these species and that would benefit from their introduction. He has estimated /15/ that an increased productivity resulting from their introduction would have a value of > $200 million (NZ) per year.

Deliberate introduction of earthworms to promote soil fertility has not been widely practised. Apart from the New Zealand experiments, peregrine lumbricids have been deliberately introduced and beneficial effects on soils and plant growth have been recorded in irrigated pasture lands in southern

Australia /2/, in pastures on reclaimed polder lands in the Netherlands/18/ and in orchards and croplands in irrigated desert regions of the USSR /5,6/.

The New Zealand experience indicates that the lumbricid species that happen to have been introduced there from the cool temperate regions of northern and western Europe are particularly well-adapted to the soils of the cool to warm temperate climate of New Zealand. This does not preclude the possibility that there are other species of earthworms, that have not by accident been introduced to New Zealand, that might be more effective in promoting soil fertility and plant growth. More obvious mismatches can be defined where the origin of introduced earthworms and the new regions they enter, which are determined by human migration patterns, have very different climates and soils.

For example, the mediterranean climatic zones of southern Australia and southern Africa were settled by immigrants from the cool temperate regions of Great Britain and northwestern Europe, who accidentally introduced the same range of lumbricid species as was introduced to New Zealand. They are poorly adapted to mediterranean climatic regimes, especially to the long summer droughts; population densities are low, usually $< 100/m^2$, unless the land is irrigated. In the mediterranean region of southern Europe and northern Africa there are other species of Lumbricidae, native to that region, that live in grasslands and are apparently well-adapted to the climatic regime. They feed and deposit their casts at the soil surface and probably influence soil fertility in the same ways as do the northern European species in moist cool temperate regions. Little is known of their ecology, behaviour or physiology, but it seems likely that a soundly based investigation of their biology could lead to selection of species that would benefit soil fertility and plant productivity in other mediterranean regions.

Selection of Intraspecific Genetic Strains. Knowledge of the cytogenetics of earthworms is confined to studies of a limited range of species of the family Lumbricidae. Omodeo /10/, who studied 14 lumbricid species, found basic (haploid) chromosome numbers of 11, 16, 17 and 18, with 18 recorded in 10 of the species. He concluded that the ancestral chromosome number of the family Lumbricidae is probably 18, and that the other numbers are probably derived from 18 by centromere fusion in some chromosomes. He also noted a high proportion of polyploid forms, with chromosome numbers 3n,4n, 6n, 8n and 10n among the species he examined and among lumbricids studied previously by Muldal /9/. Polyploidy is commonly associated with obligatory parthenogenesis, associated with premeiotic doubling of the chromosome number of the developing oocyte and abortive spermatogenesis. Omodeo /10/ demonstrated that parthenogenesis was obligatory in 8 out of 12 polyploid races of seven species; these included all four races with chromosome number 3n, two of five races with 4n, and both of those with 6n and 8n, respectively. Morphological differences between polyploid mutants within individual species were considered by Omodeo not to be beyond the acceptable limits of variability within the species. He noted that species with polyploid parthenogenetic mutants appear to be prevalent among the most widespread of peregrine lumbricid species; those that he identified included the very widespread *Aporrectodea caliginosa trapezoides*, *A.rosea*, *Bimastos tenuis*,*Dendrodrilus rubidus*, *Eiseniella tetraedra* and *Octolasion cyaneum*.

Recent investigations of ploidy and parthenogenesis in *A.caliginosa* were reported by Bidoli et al. /3/. Using enzyme electrophoresis they distinguished *A.caliginosa typica*, which is always diploid and amphigonic,from *A.caliginosa trapezoides*, which is usually triploid or tetraploid and parthenogenetic. Two samples of diploids from NE Italy were very similar, but differed markedly from diploids from northern England. Three samples of triploids from NE Italy, central Italy and Algeria were similar, but differed markedly from diploids. Parthenogenetic populations (triploids) were shown to comprise many different clines and displayed a high level of genetic variability. Terhivuo et al. /17/ distinguished 147 genotypes among 428 individuals of *Dendrobaena octaedra* collected from 85 localities along transects from northern Norway to southern Finland; eighteen genotypes made up > 50% of all individuals. Much genetic diversity was shown between and within most populations, indicating the possibility of mixed parthenogenetic and biparental reproduction. At three sample localities all individuals were genetically alike, suggesting parthenogenesis and clonal ancestry.

Clonal diversity was investigated by Jaenike et al. /7/, using electrophoresis, in the obligatorily parthenogenetic *Octolasion tyrtaeum* and in parthenogenetic pentaploid populations of *Dendrodrilus rubidus*, which includes sexual and parthenogenetic forms. Absence of biparental reproduction in *O.tyrtaeum* was taken to indicate that parthenogenesis has been longer established in this species than in *D.rubidus*. Eight clones of *O.tyrtaeum* and 31 clones of *D.rubidus* were recognized among populations from the north-eastern United States. Several measures of clonal diversity indicated that *D.rubidus* is over three times as clonally variable as is *O.tyrtaeum*, at both within- and between-site levels. Jaenike et al. /7/ postulated that clonal diversity will be high at the initial stages of derivation of parthenogenetic clones from biparental forms, and will continue to be high while biparental reproduction continues, as in *D.rubidus*. If the sexually reproducing component of a species is lost,as in *O.tyrtaeum*, an equilibrium level of clonal diversity will be attained. This level will depend on rates of genetic variation and extinction among clones; genetic variation will be low compared with that in sexually reproducing morphs, so that diversity will tend to fall to a new equilibrium level determined by ecological factors.

The existence of biparental and parthenogenetic morphs, and of high levels of clonal diversity in the latter, among some of the most widespread and successful of peregrine earthworms is well established. It is also well established that there are wide variations in behaviour and in the physiological limits of tolerance of temperature maxima and other environmental variables between populations of some of these species, that enable them to live in a wide variety of soils and climatic regimes. For example, *Aporrectodea caliginosa*, which is the most widespread and most prolific of all the peregrine earthworms in temperate agricultural and pastoral regions of the world, and is known to include diploid biparental as well as polyploid parthenogenetic morphs, includes populations in pasture soils that vary in many ways, including the following (from /8/):

a) food selection: A.caliginosa has been variously shown to be a geophage (soil-feeder) in England, a surface litter-feeder in France, a dung-feeder or dead root-feeder in Australia and in New Zealand.

b) casting behaviour: A.caliginosa deposits its casts usually at the ground surface, but sometimes below the soil surface;

c) reaction to drought: obligatory diapause, i.e., a resting stage, possibly under neurosecretory control, whose duration once it is initiated is independent of environmental stimuli, has been recognized in adult A.caliginosa in England, France and in South Africa. Quiescence, a winter resting stage that is terminated by increasing soil temperatures, has been recorded in Russia, or a summer resting stage that is terminated by autumn rains,has been recorded in Australia and in New Zealand;

d) temperature limits: LT_{50} for a population from northern United States has been shown to be c. 26°C, while for an Egyptian population it was c. 40°C.

The behavioural and physiological adaptability of A.caliginosa contribute to its success as a colonizer in a wide range of man-modified temperate environments. We should investigate the possibility that the striking ecological plasticity of this species is related to the distribution of morphs that differ in ploidy and in reproductive strategies, and to clonal diversity within polyploid-parthenogenetic morphs. Others among the most widespread of peregrine lumbricids, e.g., Aporrectodea rosea, Octolasion cyaneum, O.tyrtaeum, Bimastos tenuis, are known to include polyploid parthenogenetic morphs. Some of the most widespread non-lumbricid peregrines, e.g., Pontoscolex corethrurus and many species in the "Pheretima"-group of genera, are reported to reproduce parthenogenetically. Studies of Australian populations of P.corethrurus have shown no evidence of sperm cells in the gonads or spermathacae (B.G.M. Jamieson, pers. comm.), indicating a high probability that reproduction is parthenogenetic. It is not known whether parthenogenesis is related to polyploidy in non-lumbricid earthworms as it is in Lumbricidae, but Omodeo /10/ concluded from cytological phenomena known at gametogenesis that polyploidy is probably common in non-lumbricid families of earthworms.

Earthworms and Planet Nutrient Cycling

Paul /11/, in a discussion on the dynamics of soil organic matter,points out that in intensive agricultural systems the various organic components have the potential to act as a temporary nutrient reservoir, and that the proper management of this reservoir should make it possible to increase the efficiency of use of both soil and fertilizer nutrients. The net magnitude and general microbiology of processes such as N, P and S mineralization-immobilization are reasonably well understood, but there is little knowledge of the actual flows, pathways or in situ controls that characterize these processes. The contribution of soil animals to these processes is also acknowledged, but is as yet little understood.

Two major pathways of decomposition processes are recognized,a fast cycle that concerns utilization of low molecular weight C sources, e.g., from amino acids, mono- and oligosaccharides included in cell contents and root exudates, and a slow cycle that concerns utilization of more complex C sources. A small pool of plant nutrients, involved in the fast cycle, may circulate several times in a year through microbial cells, grazers and predators in the soil biota and through plants, while a much larger pool, contained in the bulk of the soil organic matter, is involved in the slow cycle, and much of it may be cycled through the soil biota and through plants only once in tens or hundreds of years. Paul and Juma /12/ recognized four separate pools of soil nitrogen, biomass N and non-biomass active N, together forming the fast cycling pool, stabilized N and old N, together forming the slow cycling pool. For a chernozem, Paul and Juma estimated that about 14% of the total soil N was included in the fast cycling biomass and active non-biomass pools, while the remainder was included in the slow cycling stabilized and old N pools; experimental determinations of N mineralized from this soil showed that biomass N and active non-biomass N contributed 64% of the total mineralizable N.

Anderson et al. /1/ introduced mesofauna (Collembola) or macrofauna(earthworms or millipedes) to microcosms with a substrate of forest litter. Compared with controls without animals, the rate of release of NH_4^+-N into leachates from the microcosms increased c. 60-fold with earthworms, 10-20-fold with millipedes, and 3-fold with Collembola, and that of NO_3^--N 10-fold with earthworms and 2-4-fold with Collembola.

Nitrogen is excreted by earthworms predominantly as NH_4^+-N and in urea. It is also lost through the secretion of mucoproteins, which are secreted by epidermal cells to lubricate the body surface and to maintain a moist surface layer for respiratory exchange, and in dead earthworm tissue, which contains c. 60-70% protein, i.e., c. 10-12% N, on a dry weight basis (see /8/). The quantities of N excreted, secreted and lost in dead tissue from earthworms per year may commonly be in the range 50-100 kg/ha. This nitrogen is in forms readily available to microorganisms and to plants and must be a significant component of the fast cycling pools. Its provenance is related to seasonal cycles of activity and inactivity, reproduction and mortality in earthworm populations. Dr. M.B.Bouché (pers. comm.) has recently shown that a population of earthworms dominated by Aporrectodea longa in a French pasture probably contributes c. 80% of the N requirements of the pasture during the spring, when the earthworm population attains a maximum of activity and reproduction and when the demand of nitrogen for grass growth is also at a maximum.

Recent work in New Zealand /16/ has shown that lumbricid earthworm casts from the surface of pasture soils contain about four times as much loosely-bound inorganic P and twice as much loosely-bound organic P as do underlying soils. The amount of loosely-bound P in casts increased as a function of time with incubation of the casts, indicating that at least some of the release of P was mediated by microbial activity. Satchell et al. /13,14/ found that phosphatase activity in earthworm-worked soil had peaks at pH3-5 and at pH9-10, the former peak indicating an increase in the activity of acid phosphatase, of microbial origin, and the latter an increase in the activity of alkaline phosphatase, from the earthworms.

There is a need for research to quantify the effects on plant growth of readily available N and P from earthworms. Seasonal variations in the amounts of N and P inputs, related to the phenology of earthworms and the seasonal requirements of plants, interspecific and intraspecific variability of the capabilities of earthworms to provide readily available N and P at critical times for plant growth, and selection and introduction, if necessary, of earthworms best suited to climatic variability and patterns of land use, may be expected to lead to higher levels of productivity.

Conclusion

Manipulation of earthworm populations has yielded spectacular results in some isolated cases in terms of improvements in soil structure, water infiltration, nutrient availability and plant production. Up to now these results have been achieved empirically.

There is a possibility for selection first of species and then of genotypes within species that have inherent advantages in selected environments, and for deliberate introduction of the most suitable varieties instead of the largely accidental patterns of dispersal and introduction that have prevailed in the past.

It should be possible, with a good knowledge of the physical environment, soils, and the optimum requirements for growth of crops or pastures, combined with a sound knowledge of the taxonomy, ecology, behaviour and physiology of earthworms, to select and introduce earthworms that are best suited to particular patterns of land use.

We should appreciate that opportunities exist among tropical earthworms as well as among the European lumbricids, althought we know less about the tropical earthworms than we do about lumbricids and would need to increase our understanding especially of the common tropical peregrine species.

The advantages that may be gained in improvement of soil fertility, plant production, and the better utilization of fertilizers from scientifically based earthworm introductions make this perhaps the most important aim for research on earthworms.

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